

# Observations on the Fine Structure of the Gastric Parietal Cell of the Rat\*

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PLATES 75 TO 80

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## ABSTRACT

The structure of the rat parietal cell was examined by electron microscopy. The intercellular and intracellular canaliculi are lined by microvilli which are more numerous and larger than those of other gastric cells. The numerous mitochondria have closely packed cristae and a dense matrix containing opaque particles. The cytoplasmic vacuoles typical of parietal cells are part of a network of smooth surfaced tubules and vacuoles (the endoplasmic reticulum) which is intimately associated with the mitochondria and probably connected with the lumen of the canaliculi. Only a few dense particles are found attached to the surface of these tubules. The structure of the parietal cell is compared with that of other cells whose function also is transport of inorganic ions and water. Evidence is presented supporting the hypothesis that parietal cells differentiate from a less structurally specialized cell in the neck region of the gastric gland.

## INTRODUCTION

The parietal cell of the gastric mucosa has been extensively studied by light microscopy (Bensley, 1932; Plenk, 1932). Because its function appears to be limited solely to the secretion of hydrochloric acid and water, it represents a highly specialized type of cell and is, therefore, of particular interest in the study of structure in relation to function. Several investigators have already used the electron microscope to resolve further details of the structure of these cells. Brief descriptions have been given by Dalton (1951), Sedar (1955), and Challice, Bullivant, and Scott (1957). Kurosumi *et al.* (1958) have described the parietal cell of the rat together with other gastric cell types, and Hally (1959) has given a comprehensive account of the mouse parietal cell. Reports of changes in the structure of parietal cells associated

with changes in functional state have been given by Hally (1958) and Sedar (1959).

This paper, in addition to confirming some of the observations of previous investigators, describes certain additional features of the parietal cell. Resolution of cytoplasmic constituents has been aided by the use of an epoxy resin (araldite) as an embedding medium and treatment of the sections with solutions which improve contrast in electron microscope.

## Materials and Methods

Adults rats were starved for 24 hours and killed by a blow on the head, either without refeeding or 1 to 2 hours after refeeding. The stomach was removed quickly and thin full-thickness strips were cut from the mucosa at the greater curvature close to, but not including, the cardiac zone. The strips were fixed either in 1 per cent osmium tetroxide in veronal acetate buffer (approximate pH 7.5) (Palade, 1952) with 0.25 M sucrose added (Caulfield, 1957), or in 1 per cent osmium tetroxide in potassium dichromate solution (approximate pH 7.5) (Dalton 1955). Fixation was continued for 45 to 75 minutes at 0°C. The tissues were then rinsed in 30 per cent ethanol and dehydrated in ascending concentrations of ethanol. Some strips were embedded in a mixture of six parts butyl methacrylate

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and one part methyl methacrylate with benzoyl peroxide added and prepolymerized at 60°C., and others were embedded in araldite<sup>1</sup> after removal of ethanol with toluene. In both cases the tissues were embedded in the plastic in gelatin capsules and polymerized at 60°C. Thin sections were cut on a Porter-Blum microtome, mounted on copper grids coated with collodion, and examined in an RCA EMU 2B or 2E electron microscope. Some sections were stained by floating the grid with attached sections face down on the clean surface of suitable solutions (Watson, 1958). These solutions included 4 per cent lead nitrate (approximate pH 4), 1 per cent silver nitrate (approximate pH 6), or 1 per cent potassium permanganate (approximate pH 7) all in distilled water. Both araldite- and methacrylate-embedded sections could be stained. All the agents used produced a surface precipitate on the section but in some sections this was minimal, especially with lead nitrate. The increased information which could be obtained from the micrographs of stained sections was considerable, especially with araldite-embedded sections which inherently have low contrast. Thicker sections were examined by means of the phase contrast microscope or they were stained for light microscopy.

#### RESULTS

*General.*—The structure of the parietal cell of the rat corresponds closely to that of the mouse as described by Hally (1959). The cell is usually pyramidal with its apex directed towards the lumen. The relationship to the lumen varies with the cell's depth in the gastric gland and with its functional state. Only a small part of the cell directly contacts the lumen, but the surface area of this part is expanded by means of intercellular and intracellular canaliculi. The apical surface, where it is exposed, as well as the surface of the canaliculi are covered closely by microvilli which are more profuse and larger than those of any other gastric cell (Fig. 1). These structures are well demonstrated in electron micrographs, as shown by other authors (Dalton, 1951; Sedar, 1955; Challice, Bullivant, and Scott, 1957; Kurosumi *et al.*, 1958; Hally, 1959). In parts of some tissue blocks the parietal cells showed smooth surfaced projections into the lumen from their apical surfaces. This finding was associated with other signs of poor fixation and can be explained by autolysis and rupture of the cell membrane *post mortem*. The lumen of the canaliculus is often almost obliterated by close interdigitation of

microvilli but occasionally may be dilated, with separation of the microvilli. Extreme dilatation of the canaliculi may be a distortion produced by tissue processing. Each microvillus consists of a dense cortex lying immediately below the surface membrane and a central less dense core. The junction between core and cortex may be delineated by a slight increase of density appearing as dots or elongated particles (Fig. 2). These apparently are sections of a fibrillar network perhaps consisting of precipitated protein. They do not form a continuous membrane and the additional or third membrane described by Hally (1959) could not be demonstrated. The surface of the microvillus is always of similar density to other plasma membranes although more dense than the membranes of the vacuole system or the membranes with attached particles. Occasionally, the surface membrane was resolved into two parallel dense lines.

The basal surface of the cell is covered by a thin continuous basement membrane (Fig. 9). Infoldings of the plasma membrane occur at the basal surface of the cell but are poorly developed, penetrating only a short distance. The infoldings are not accompanied by basement membrane. The cytoplasm at the borders of the cell and around the intracellular canaliculi is more dense than the ground cytoplasm elsewhere in the cell which has a characteristically low density (Fig. 2).

The plasma membrane at the lateral boundary of the cell is often thickened near the lumen to form a terminal bar (Fig. 6). The degree of interdigitation with neighboring cells varies and appears to be influenced by the nature of the adjacent cell. The surface epithelial and neck mucous cells apparently induce extensive interdigitation since where the parietal cell contacts another parietal cell or a chief cell the borders are relatively straight. Often an intercellular canaliculus separates parts of the lateral border of the parietal cell from its neighbor, and in these regions the lateral surface bears microvilli.

*Mitochondria.*—The mitochondria are a predominant component of the parietal cell. They are dense oval bodies or short rods whose average diameter (approximately 0.6  $\mu$ ) is greater here than in other gastric cells. Cristae are numerous and as many as thirty cristae have been counted within a span of 1  $\mu$ . This spacing agrees closely with that observed in the mouse parietal cell (Hally, 1959). The distance between the centers of the membranes forming a crista has a relatively constant minimum in the range of 15 m $\mu$  in

<sup>1</sup> Araldite was obtained from the New York Society of Electron Microscopists.

sections at right angles to the membranes. The external membrane pair has a more variable and often smaller spacing. Cristae may lie at any angle to the long axis of the mitochondrion and may curve, branch, or anastomose with each other. Areas of branching and anastomosis may have led to the report that some mitochondrial cristae in the parietal cell are of the villous type (Kurosumi *et al.*, 1958).

The dense matrix and the small dense particles within these mitochondria have already been reported (Chalice, Bullivant, and Scott, 1957). The dense particles lie in the matrix between the cristae and are often situated in small pockets caused by divergence, branching, or termination of cristae (Fig. 3.). They may reach a diameter of 25  $\mu$ , but are rarely larger. In the micrographs obtained in this study no internal structure could be detected in these particles.

The mitochondria, as in the mouse parietal cell, tend to be distributed in two groups, one towards the lateral and basal borders of the cell and one in the vicinity of the nucleus (Fig. 1). These groups are separated by a region of pale cytoplasm containing the intracellular canaliculi. In the majority of parietal cells this area is crowded with small vacuoles.

*Microbodies.*—Amongst the mitochondria lie a number of inclusions usually smaller than mitochondria and with small dense particles or dense masses often with pale areas included. They are oval or sometimes irregular, usually without a discernible membrane, but occasionally showing an indistinct membrane partly or completely enclosing them. Similar bodies are seen in all the epithelial and glandular cells of the gastric mucosa but they are most numerous in the parietal cells (Fig. 3). These inclusions are probably identical with similar structures in renal tubules called microbodies by Rhodin (1954). Thicker sections from which the plastic has been removed and which have been stained by the periodic acid-Schiff technique contain stained granules in the parietal cells. These are believed to be identical with the microbodies.

*Cytoplasmic Vacuoles and Tubules.*—Cytoplasmic vacuoles are a characteristic feature of the rat-parietal cell. They appear in sections as small circular profiles bounded by a smooth membrane and containing a material of low electron density and are situated chiefly in the neighborhood of intracellular canaliculi. Their shape and size varies somewhat, being regularly circular in out-

line and with very little intervening cytoplasm in some cells; whereas in other cells they are smaller, more irregular in outline, and spaced further apart. Part of the variation is a reflection of differences among living cells, but extreme dilatation is often associated with dilatation of canaliculi, shrinkage of cells with increase of intercellular spaces, and other indications of tissue damage. The maximum diameter of the vacuoles in tissues apparently well preserved is approximately 200  $\mu$ . In most preparations, traces of other membranous structures can be detected between these vacuoles and, under favorable circumstances, may be resolved into a system of small tubules whose diameter is approximately 20  $\mu$  and which run in many directions throughout the cell. Frequently, parts of these tubules are intimately associated with mitochondria (Fig. 5). Occasionally, a vacuole and a tubule appear to be interconnected (Fig. 5). The smooth membraned tubules are similar in diameter and in thickness and density of their walls to those whose attached dense particles identify them as "rough surfaced endoplasmic reticulum" or "ergastoplasmic membranes." Rarely groups of flattened vacuoles occur which resemble in structure the Golgi region of other cells (Fig. 4).

*Membranes with attached particles* are not abundant. They are scattered throughout the cytoplasm, but more concentrated near the basal border and near the nucleus. The paucity of elongated profiles and the frequency of small circular arrangements of particles (often giving an impression of free particles but bounded by a faint circular membrane) suggest that these membranes, like the smooth surfaced forms described above, are not flattened sacs but tubules. When one of these tubules is sectioned longitudinally, the particles are often found in small groups separated by a considerable length of membrane without particles (Fig. 2). Some of the membranes with attached particles appear to be closely associated with the outer nuclear membrane, as has been described in other cells.

*Vacuole-Containing Bodies.*—In each cross-section of a parietal cell one or two structures consisting of a circular smooth membrane containing smaller circular profiles are present (Fig. 7). They have been reported in the mouse parietal cell by Hally (1959), who called them "vacuole-containing bodies" and identified them with similar structures described by Rhodin and Dahlman (1956) in the tracheal epithelium. They

have not been identified in other cells of the gastric mucosa.

*Tonofibrils.*—Occasionally, a bundle of fine filaments can be seen in the cytoplasm sometimes related to the canaliculi (Fig. 8). These fibrils are reminiscent of the tonofilaments which are more prominent in some other epithelial cells (Odland, 1958).

*Nucleus.*—The nucleus of the parietal cell tends to be centrally placed and circular. Its density is less than that of other nuclei of the mucosa except for those of the surface epithelial cells. The nuclear membrane is double, and in a few places groups of particles are attached to it; but throughout most of its extent it is free from attached particles.

*Neck Parietal Cells.*—At the region of junction of the gastric pits and the gastric glands, parietal cells are found with somewhat different characteristics from those described above, which are found deeper in the gland. The general cytoplasmic density is lower and the cytoplasmic vacuoles are considerably reduced in number, but the granular membranes are more prominent. The mitochondria appear to be less numerous and more widely spaced. The intracellular canaliculi are closed and may be less extensive than in deeper cells (Fig. 10). Transitions occur between this type of cell and the more numerous deeper type.

#### DISCUSSION

In this investigation certain structural features of the parietal cell showed considerable variation among individual cells. Some of this variation could be attributed to tissue damage during processing. Both in starved and in starved and refed rats, where the usual criteria for assessing preservation of tissue details were best satisfied, the intracellular canaliculi were almost, or completely collapsed and the cytoplasmic vacuoles only moderately distended. This is probably their condition shortly after death. In these areas greatly distended canaliculi and vacuoles were not observed; neither were the smooth surfaced projections into the lumen described by Kurosumi *et al.* (1958), although these changes were seen in areas thought to be inadequately preserved.

It is generally accepted that the parietal cell secretes water, hydrogen ions, and chloride ions, but does not participate in the synthesis of the protein constituents of the gastric juice. "Consistent with this concept and with the low affinity

for basic dyes displayed by parietal cells is the small number of basophilic particles associated with protein synthesis and containing ribose nucleic acid." (Palade and Siekevitz, 1956).

The cell has certain specializations such as microvilli and abundant mitochondria which are possessed by other cells believed to be concerned primarily with the transport of water and inorganic ions. The parietal cell microvillus shows a marked differentiation of its cytoplasm into a cortical zone and a core which is not as obvious in the microvillus of the renal tubule or the intestinal epithelium. This may be explained by the greater density of the cytoplasmic matrix in the latter cells, so that the core and cortex are of similar density. However, a line of demarcation can sometimes be seen in the intestinal microvilli comparable to that between core and cortex in the parietal cell.

The numerous mitochondria presumably possessing oxidative enzymes are consistent with the need for a steady supply of energy for transporting ions against a concentration gradient for long periods without exhaustion. Small dense particles in the matrix of mitochondria are numerous in parietal cells, renal tubule cells, and the salivary duct cells. Their location at points of branching and termination of mitochondrial cristae suggests that they are structural components and not artefacts. Drinking salt solutions increases the number of these particles in the mitochondria of the intestinal epithelium (Weiss, 1955), and it has been suggested that they are associated with the transport of inorganic ions. They have also been reported in many other cell types. The closely packed cristae and dense matrix also suggest a high metabolic activity.

In renal tubule cells and salivary duct cells (Pease, 1956) the mitochondria are elongated and closely associated with infoldings of the lateral and basal plasma membrane of the cell. Parietal cell mitochondria are short, more widely distributed, and not associated with the plasma membrane, which has only minor infoldings confined to the basal surface. The parietal cell mitochondria are closely associated with a small tubular component of the cytoplasm which has not been described in the parietal cell by other authors. Although Kurosumi *et al.* (1958) and Hally (1959) both state that the cytoplasmic vacuoles so conspicuous in these cells are completely isolated from each other, the results reported here suggest that the vacuoles are in-

terconnected by small tubules to form a randomly oriented system, which supports the identification of these vacuoles as a diffuse type of endoplasmic reticulum by Sedar (1955). Although sites of junction between tubules and vacuoles were seen only rarely, the dimensions of the system and the tortuous course of the tubules make it unlikely that a section 20 to 40  $m\mu$  thick would include a vacuole and sufficient length of conjoined tubule to make identification positive. The membrane enclosing the vacuoles, the smooth walled tubules, and the membranes with attached granules could not be differentiated from each other by thickness or density even after selective staining of the section with various solutions. The diameter of the two types of tubules was similar, and it can be assumed that granules and vacuoles are local variations of an interconnected system (Palade and Siekevitz, 1956). The tubule system is dispersed and, although occasionally a mass of somewhat flattened vacuoles may show some resemblance to the Golgi structure of other cells (Fig. 4), it is never as concentrated as in the more typical Golgi zone.

The nature of the connection, if there is one, between this system and the canaliculi could not be identified with certainty, but an appearance indicating junction of a small tubule with a cleft between adjacent microvilli was sometimes observed. However, sections through the canaliculi are difficult to interpret because of the complex orientation of the microvilli. No clear evidence was found that the cytoplasmic vacuoles discharged their contents directly by rupturing into the lumen of the canaliculi.

The poor ability of the parietal cell to induce interdigitations with neighboring cells contrasts with the extensive interdigitations induced by surface epithelial cells which must withstand abrasion from the ingestion when they have migrated to the surface of the mucosa.

The presence of parietal cells in the neck region of the gastric glands that appear to be less differentiated than those situated more deeply in the mucosa lends some support to the hypothesis that these cells do not divide, but differentiate from epithelial cells in this region and then migrate away from the surface of the mucosa. Normal mitosis and arrested mitosis after co-chicine administration can be found in cells in this region, but are rarely, if ever, seen in parietal or chief cells (Leblond and Walker, 1956). The use of tritiated thymidine to label dividing

cells also supports this hypothesis (Hughes *et al.*, 1958). It has been suggested that the rate of mitosis increases after feeding (Hunt, 1954) so that the possibility of an increase in the number of this type of cell must be considered when studying the effects of variation in functional state on the structure of the parietal cell.

This investigation revealed further complications in the structure of the parietal cells. More information is needed, in particular, concerning the beginning and ending of the tubule system, its exact relationship to the mitochondria, and the nature of the contents of the cytoplasmic vacuoles. There is, at present, no evidence to determine the relative importance of the tubule system and of the surface membrane of the microvilli in the secretion of hydrochloric acid. However, it may be significant that the tubules are more closely associated with the mitochondria than are the microvilli.

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## EXPLANATION OF PLATES

FIGS. 1 and 10, Palade's fixative, methacrylate method.

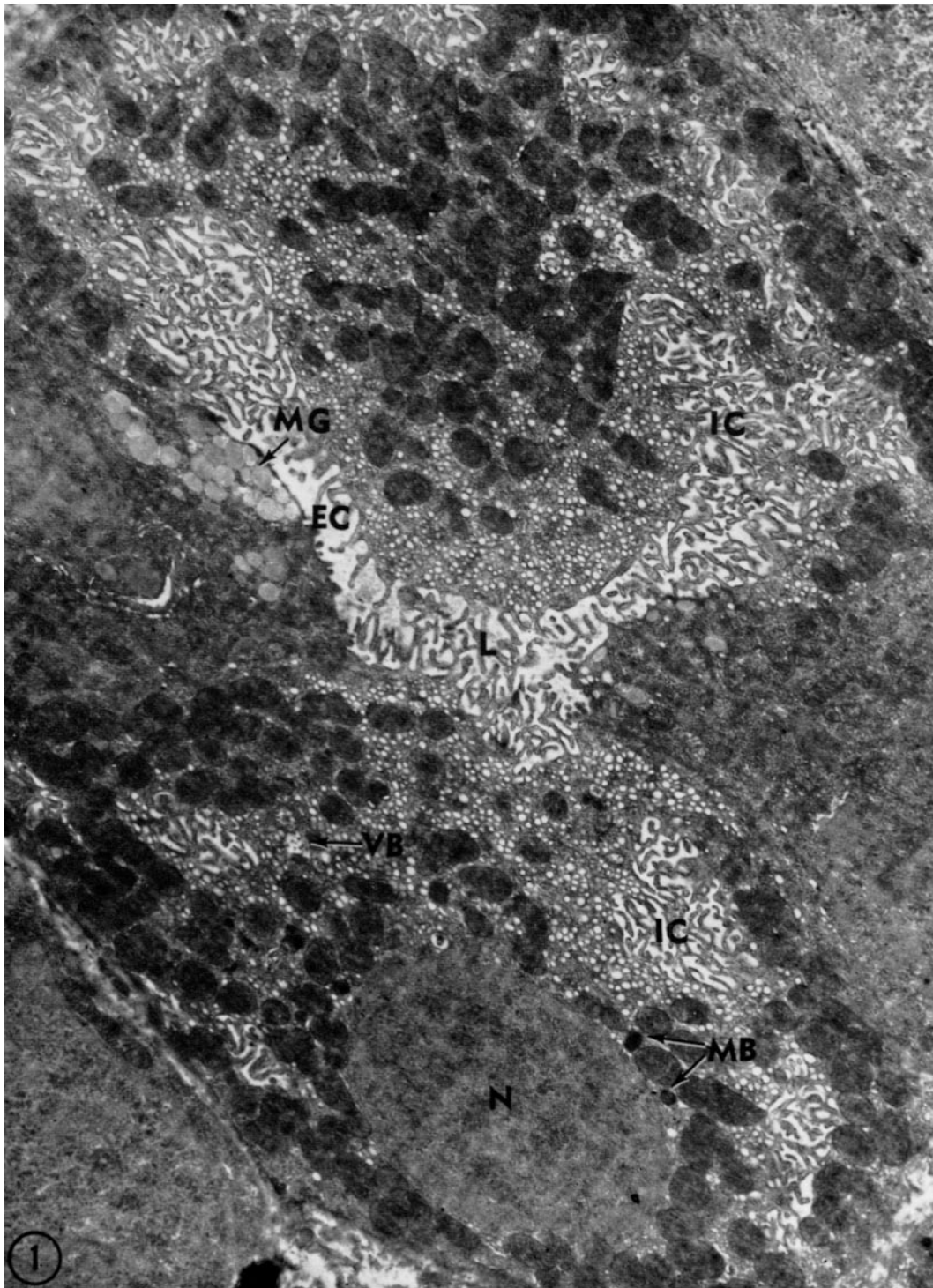
FIGS. 2, 3, 4, and 5, Dalton's fixative, araldite-embedded, section treated with lead nitrate solution.

FIGS. 6 and 7, Palade's fixative, methacrylate-embedded, section treated with silver nitrate solution.

FIGS. 8 and 9, Palade's fixative, araldite-embedded, section treated with potassium permanganate solution.

## PLATE 75

FIG. 1. Part of a cross-section of a gastric gland of a starved rat. Two parietal cells are situated one above and the other below the lumen (L). They are separated laterally by two surface epithelial cells containing mucous secretion granules (MG). In the upper parietal cell intercellular (EC) and intracellular (IC) canaliculi are sectioned longitudinally. In the lower parietal cell the canaliculi are sectioned transversely and the section includes the nucleus (N), microbodies (MB), vacuole-containing bodies (VB), numerous large dense mitochondria, and small pale cytoplasmic vacuoles. Microvilli cover the surface of the parietal cells.  $\times 6,600$ .



(Lawn: Fine structure of gastric parietal cell)

PLATE 76

FIG. 2. A section through the basal border of a parietal cell of a recently fed rat. This surface is covered by a basement membrane (*BM*) and possesses a region of infolding of the cell membrane (*I*). To the left is an intracellular canaliculus (*C*) with microvilli. At the arrows (*I'*) are regions where the fibrillar layer between core and cortex of the microvilli can be seen. At *T* a small tubule with associated dense particles is sectioned longitudinally. Note that the dense particles occur in widely separated groups on an otherwise smooth membrane.  $\times 60,000$ .

FIG. 3. Part of a parietal cell of a recently fed rat. A mitochondrion (upper right) contains branching cristae. Between the cristae are three dense particles. A group of microbodies are seen at lower left (*MB*). Small tubules, in some areas associated with dense particles, and a few pale vacuoles are scattered in the cytoplasm. At the arrow two vacuoles appear to join.  $\times 60,000$ .



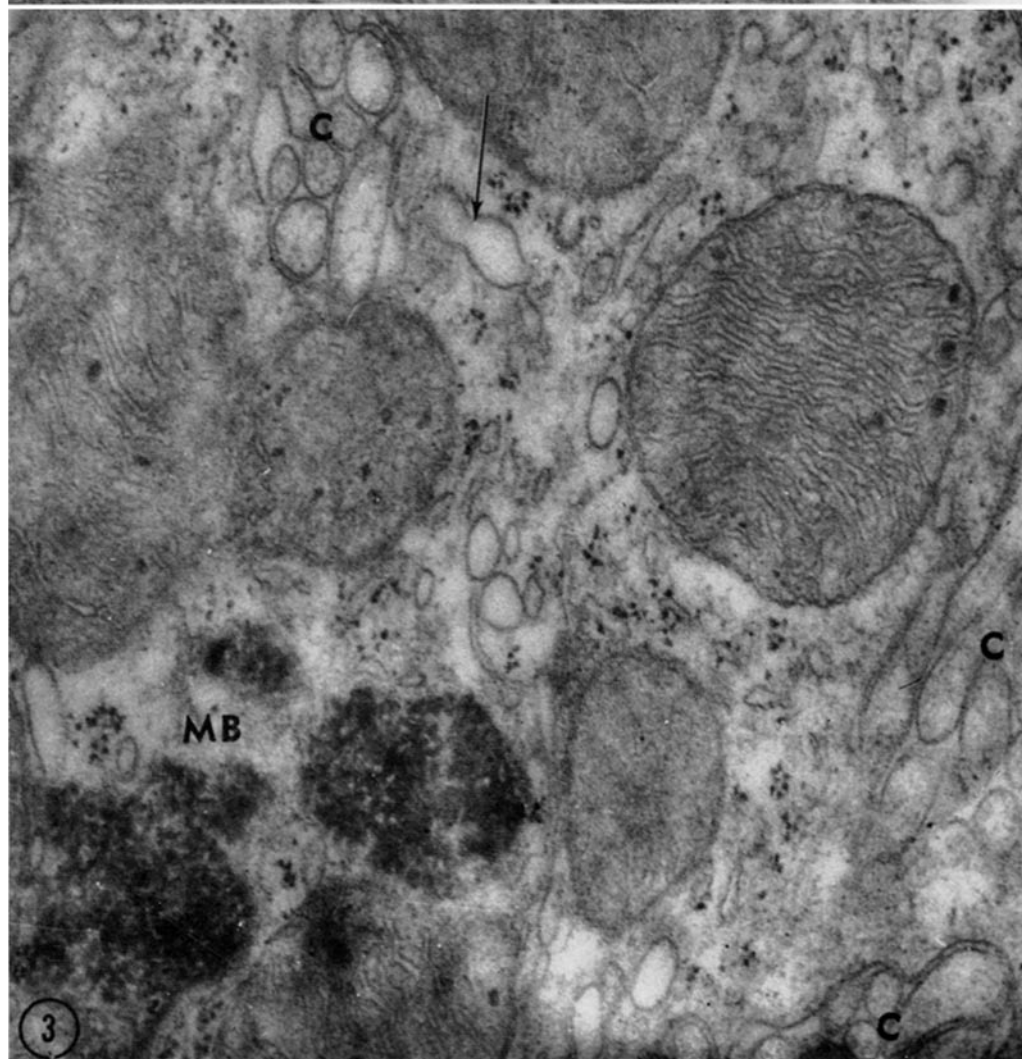
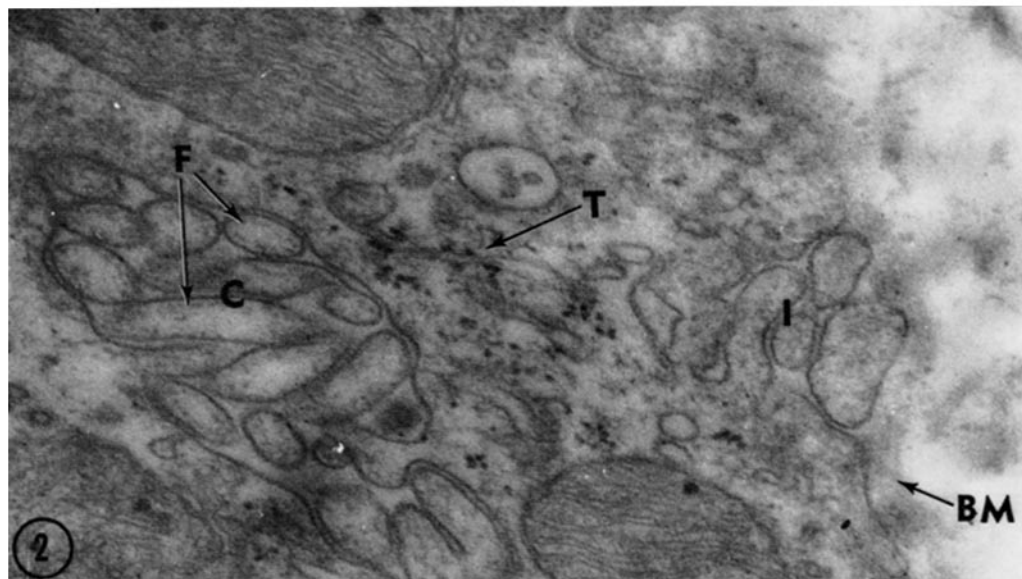


PLATE 77

FIG. 4. This section of a parietal cell (recently fed rat) contains a group of slightly flattened vacuoles (*G*) which has some resemblance to the typical Golgi apparatus of other cells.  $\times 40,000$ .

FIG. 5. A small portion of a chief cell is included at lower right, separated from part of a parietal cell (above) by an intercellular canaliculus (*EC*). An intracellular canaliculus is sectioned at *I.C.* In the center a tubule appears to join a vacuole (*J*). Note the close relationship of tubules and vacuoles to the mitochondria (*T*) (recently fed rat).  $\times 60,000$ .

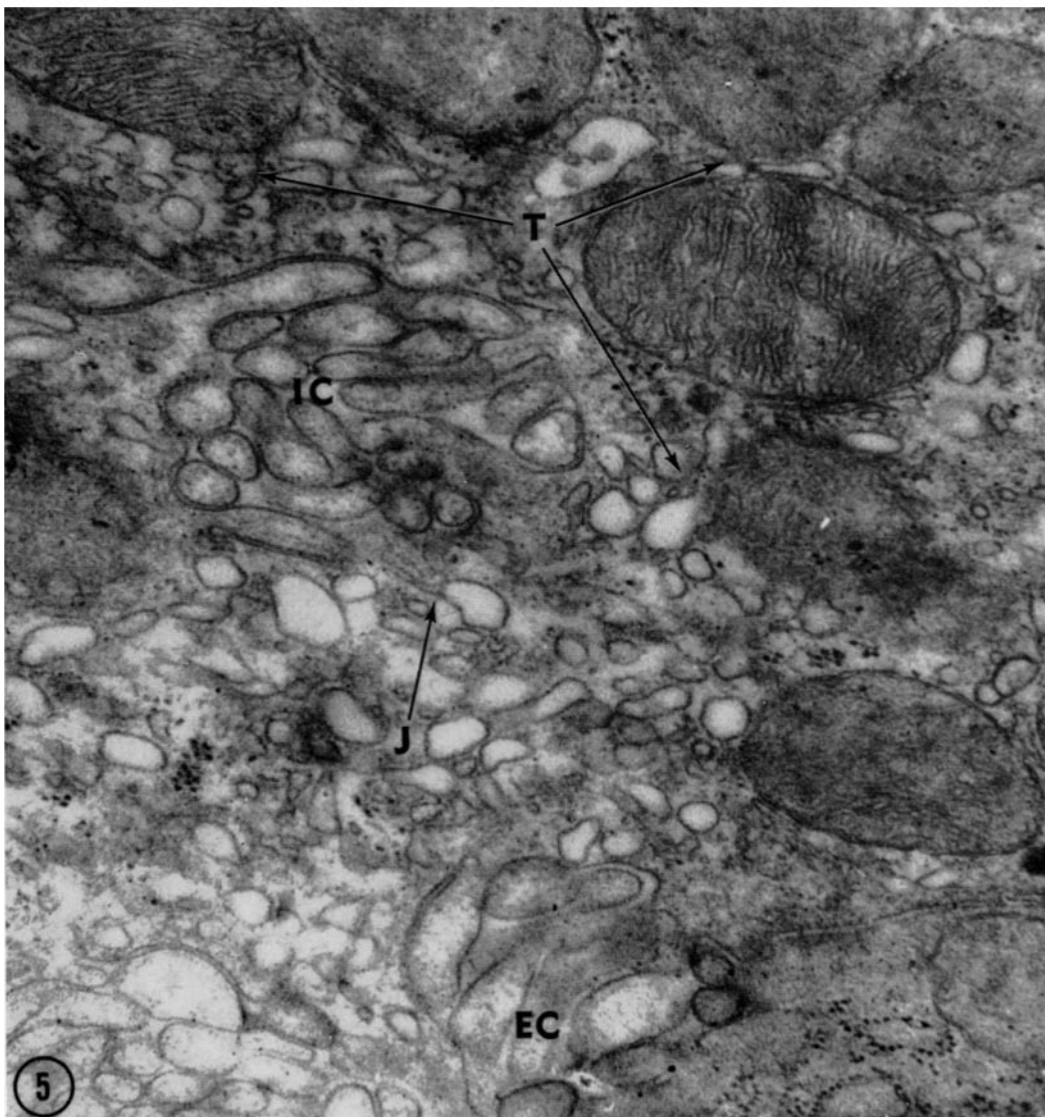
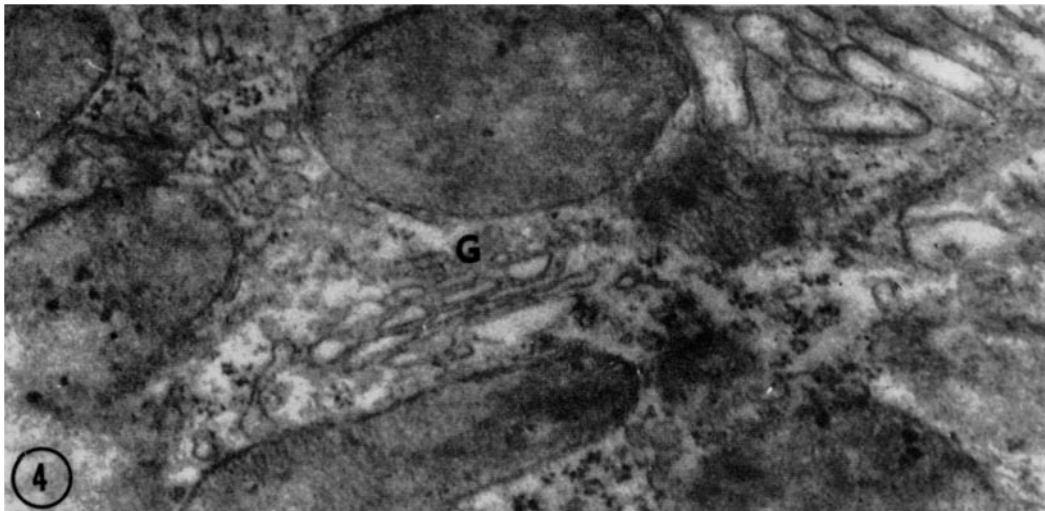
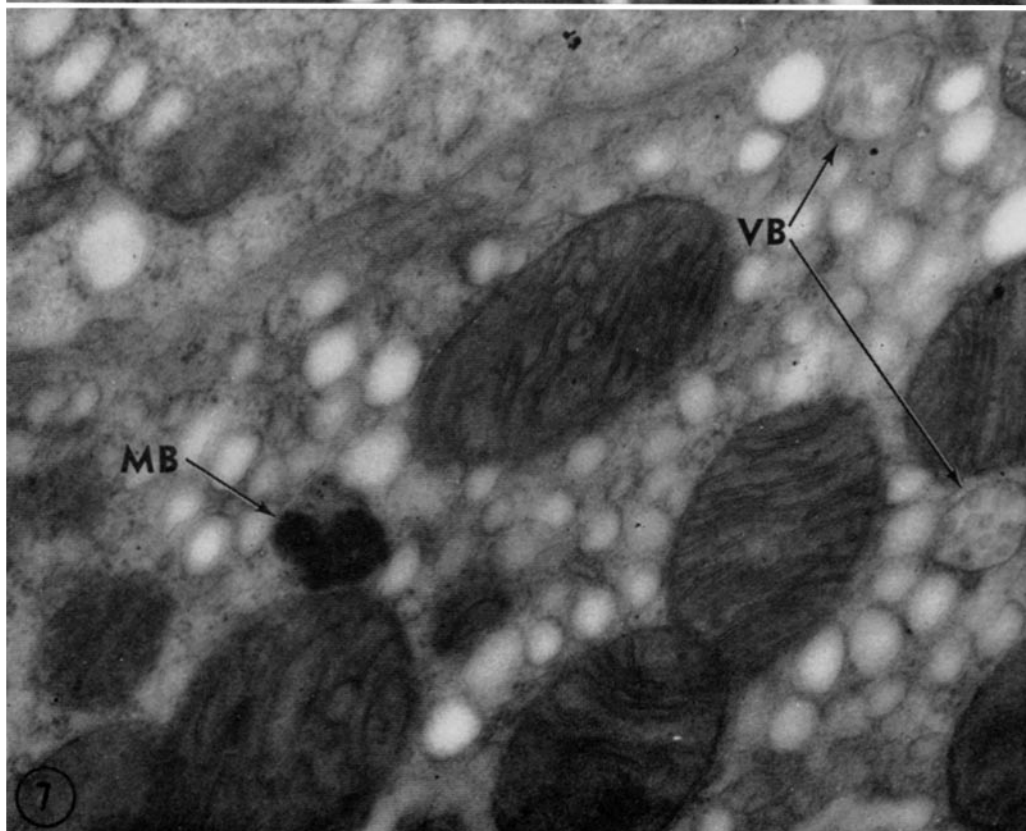
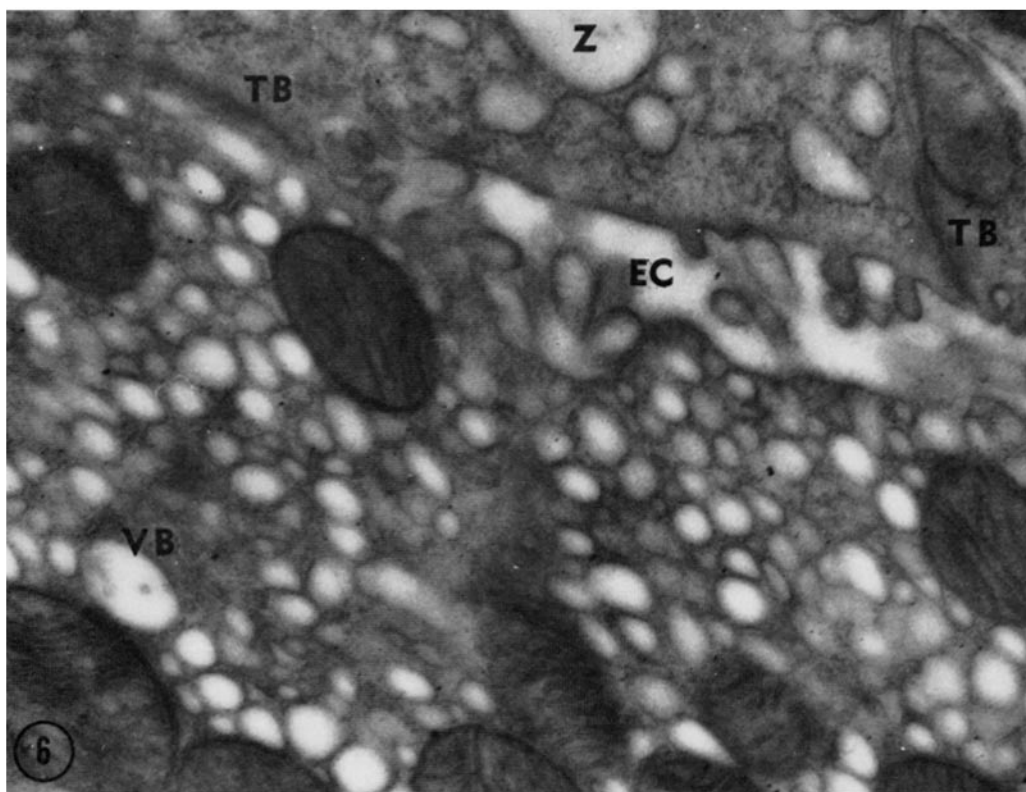


PLATE 78

FIG. 6. An intercellular canaliculus (*EC*) separates two chief cells (above) from a parietal cell (below). Between the apical parts of the cells thickenings of the cell membranes can be seen of the terminal bar type (*TB*). The cytoplasmic membranes of the chief cells with their numerous attached particles contrast with the smooth walled tubules and vacuoles of the parietal cell. The microvilli of the parietal cell are longer than those of the chief cells (starved rat). (*Z*, zymogen granule.)  $\times 24,000$ .

FIG. 7. A chief cell (upper left) adjoins a parietal cell. The cell border between them is relatively straight. The parietal cell contains two vacuole containing bodies (*VB*) and a microbody (*MB*) and the cytoplasmic tubules and vacuoles are prominent. In the mitochondrion at the center the cristae anastomose and branch (starved rat).  $\times 40,000$ .

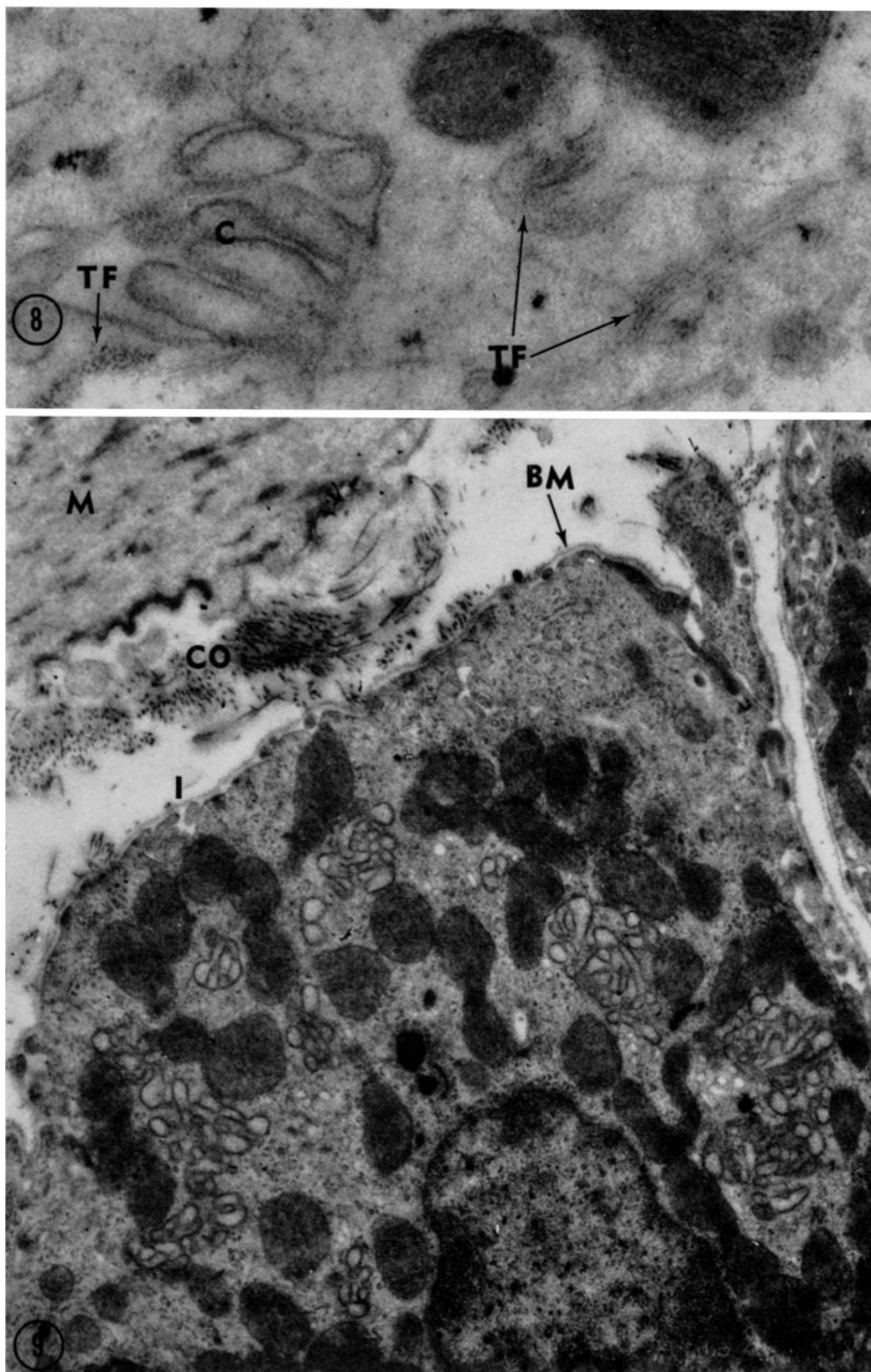


(Lawn: Fine structure of gastric parietal cell)

PLATE 79

FIG. 8. Treatment of this section with potassium permanganate solution has increased the contrast of the tonofilaments (*TF*) grouped to form tonofibrils in the parietal cell cytoplasm. On the left a tonofibril is sectioned transversely, and on the right are portions of tonofibrils sectioned longitudinally (recently fed rat).  $\times 60,000$ .

FIG. 9. The basal surface of this parietal cell is covered by a thin continuous basement membrane (*BM*) which passes over the basal infoldings of the surface membrane (*I*). Bundles of collagen fibres (*CO*) lie in the interstitial space. The cytoplasm of the parietal cell has dense mitochondria and intracellular canaliculi. The nucleus is included in the section. At the upper left (*M*) is part of one of the smooth muscle cells occasionally found between the gastric glands (recently fed rat).  $\times 12,000$ .

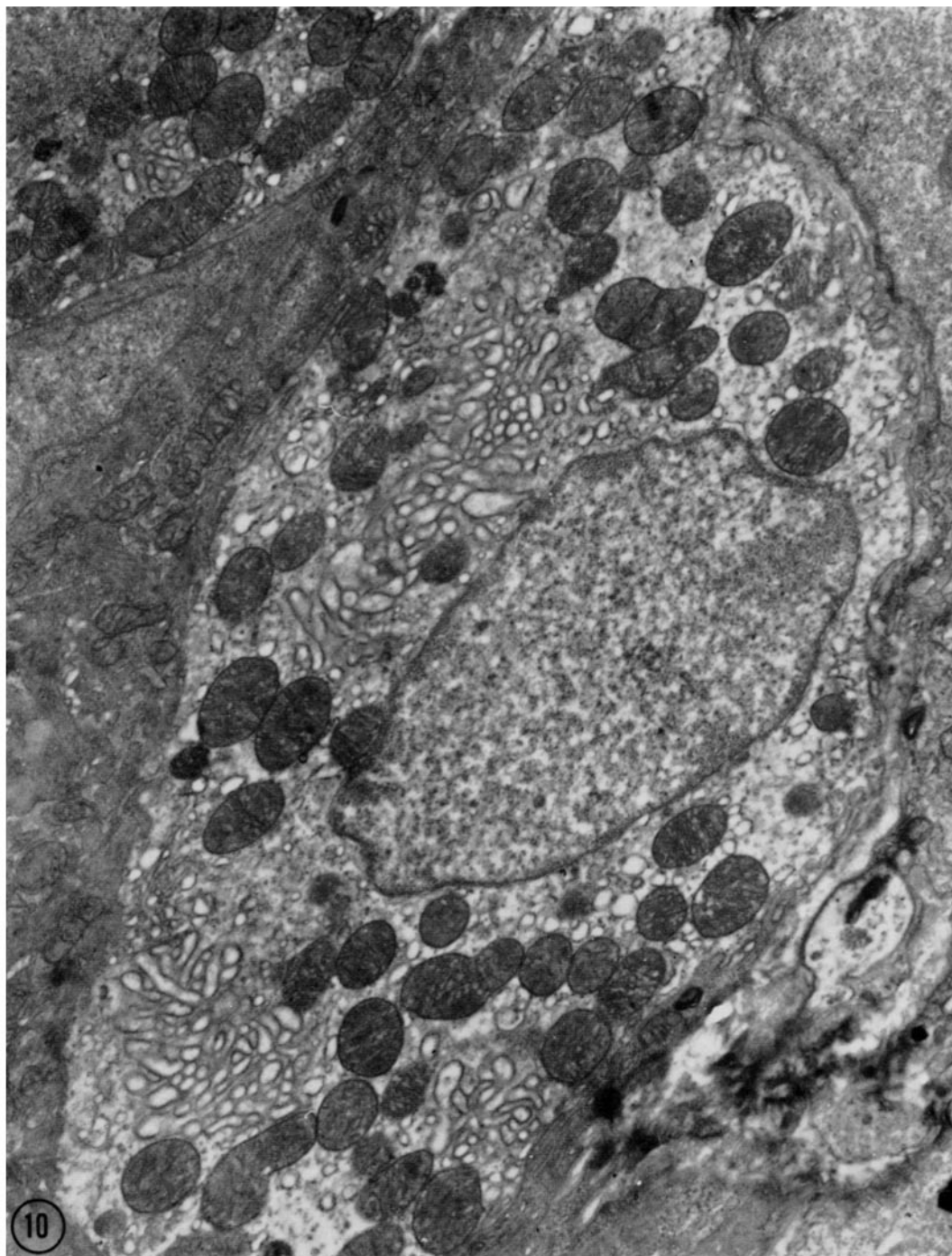


(Lawn: Fine structure of gastric parietal cell)

PLATE 80

FIG. 10. A parietal cell from the base of a gastric pit of a starved rat. The cytoplasm is pale, and the mitochondria and cytoplasmic vacuoles are less numerous than in a corresponding section through a cell lying deeper in the mucosa. The canaliculi are collapsed.





(Lawn: Fine structure of gastric parietal cell)